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Overshadowing of geometry learning by discrete landmarks in the water maze: Effects of relative salience and relative validity of competing cues

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Abstract

The effects of stimulus salience and cue validity in the overshadowing of the geometric features of an enclosed arena by discrete landmarks were investigated in rats using the water maze paradigm. Experiment 1 established that in a rhomboid-shaped arena the acute corner was more salient than the obtuse corner for the rats. In the subsequent two experiments, the rats were trained to find a submerged platform either in an acute corner or in an obtuse corner. In addition to the corner angle, the platform was also signalled by the concurrent presence of a discrete landmark which was a more valid cue for the platform in Experiment 2. The presence of the landmark resulted in an overall overshadowing of geometry learning, and the effect tended to be greater when the platform was at the obtuse corner than at the acute corner. Experiment 3 extended the finding by showing that the presence of landmarks, which were made equally valid as the angles, still overshadowed learning about geometry, but critically only when the platform was found at the obtuse corner, not the acute corner. These results demonstrate for the first time that learning about geometry can be overshadowed by the presence of discrete landmarks, and also that whether such overshadowing is observed depends on the stimulus salience and the relative validity of the competing cues. These findings imply that learning based on the geometry of an environment follows the same basic rules that apply to a wide range of other learning paradigms.

KEYWORDS: Cue competition, Associative learning, Geometry, Spatial learning, Water maze

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When animals learn to predict the occurrence of a biologically significant event in their environment, they can learn not only a single relationship between a predictive stimulus and its consequent event but also relationships between multiple cues that are simultaneously present and their common consequence. In learning such multiple CS-US relationships, it is often found that animals learn less about each individual CS when the CS is presented in conjunction with another CS than when the same CS is presented on its own (e.g. Kamin, 1969; Pavlov, 1927). This phenomenon, called overshadowing, has been consistently observed in a wide variety of testing procedures and species (Mackintosh, 1974).

One exception to the seemingly ubiquitous nature of the overshadowing effect, however, can be found when animals are trained to navigate to a certain location within an enclosed environment with a specific shape, i.e. spatial learning with reference to the geometry of an environment. A number of studies so far have found that learning about the location of a goal based on the geometry of an enclosed arena is not restricted by the concurrent presence of other types of cues, such as a discrete landmark located near the platform (Doeller & Burgess, 2008; Hayward, Good, & Pearce, 2004; Hayward, McGregor, Good, & Pearce, 2003; McGregor, Horne, Esber, & Pearce, 2009; Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001; Wall, Botly, Black, & Shettleworth, 2004; see Pearce, 2009 for a review). McGregor et al. (2009), for example, trained rats to find a hidden platform in one of the base corners of an isosceles triangular arena. An experimental group of rats was trained with a single landmark always suspended above the platform, whereas a control group of rats was trained in the same way except that a second, identical landmark was also suspended at the other base corner. After both groups of animals learned the discrimination of the two corners, a test trial was conducted in the absence of any landmark and the platform. During the test, the two groups of animals searched around the location where the platform had been located previously during training for equal amounts of time, indicating that learning based on the geometric features of the triangular arena was not restricted by the presence of a landmark.

Such failures to demonstrate overshadowing can be clearly problematic for the universality of associative learning theories, many of which do not specify the type of learning that the theory can apply to, but rather are considered to constitute a general learning rule (e.g. Rescorla & Wagner, 1972). Indeed, these failures to observe overshadowing in the geometric learning paradigm have led some authors to propose that learning about the shape of the environment is governed by rules fundamentally different from those described by associative learning theories. Both Cheng (1986) and Gallistel (1990), for example, have proposed that information about the shape of the environment is encoded in a dedicated geometric module that is impervious to non-geometric information such as that provided by individual landmarks. A similar proposal by Doeller and Burgess (2008) asserts that vectors derived from a uniform boundary can be used to learn a location, and that the presence of landmarks has no influence on learning these boundary vectors. Doeller, King, and Burgess (2008) suggested the boundary-learning and landmark-learning processes were independent of one another because the neural substrates for landmark- and boundary-learning are independent: landmark-learning is governed primarily by the dorsal striatum, while boundary-learning activates the hippocampus. Related to this theory is Wang and Spelke's (2002, 2003) hypothesis that spatial learning in many animals and in humans is supported by egocentric representations of individual landmarks, together with an allocentric representation of environmental geometry that enables reorientation within the environment. When disoriented, the authors claim, animals need only refer to the overall shape of the environment to reorient themselves. Thus, in each of these theories, no matter how many landmarks surround a hidden goal, animals are assumed to learn about its location relative to the shape of the environment to the same degree as if no landmark were present.

Although there have been several recent reports showing that geometric cues can interact with information provided by the colours of the walls (Graham, Good, McGregor, & Pearce, 2006; Horne & Pearce, 2011; Pearce, Graham, Good, Jones, & McGregor, 2006), those studies do not offer an explanation as to why experiments with similar procedures fail to show cue interaction when discrete landmarks were used as non-geometric cues (e.g. McGregor et al., 2009). It might be argued that these colour cues are integrated into a representation of geometry in a way not possible for discrete landmarks, whereas learning about discrete landmarks is indeed independent of the process responsible for geometry learning as envisaged by those theories mentioned above.

Before accepting the conclusion that geometric learning is impervious to the presence of additional information provided by discrete landmarks, however, we have to consider one simple alternative account based on the salience of those cues in competition. Thus, in conditioning tasks in operant chambers, it is normally the more salient cues or easier discriminations that overshadow less salient or more difficult ones, and not vice versa (e.g. Mackintosh, 1976; Miles & Jenkins, 1973). If the same principle can apply to navigation tasks, then it is possible to argue that the geometric cues, such as walls and corners, are more salient for animals than discrete landmarks, and therefore it is more difficult for the latter to overshadow the former, without necessitating the additional assumption on the special status of geometric cues. Although McGregor et al. (2009) were aware of this possibility and demonstrated in separate experiments that the landmark they employed was salient enough to overshadow learning based on other non-geometric cues (the room cues, but not colours of the walls; Experiment 3 and 4, McGregor et al., 2009), they did not explicitly manipulate the salience of the target geometric cues, which leaves the possibility that overshadowing can still be observed when the landmark is put in conjunction with a less salient geometric stimulus.

One example of geometric features that potentially differ in their salience is offered by Tommasi and Polli (2004), who trained domestic chicks to find food in one corner of a parallelogram arena. The location of the food was signalled by the length of the wall (e.g. food is at the left-hand end of a long wall) as well as by the angle of the corner (e.g. food is at the acute angled corner). When chicks were later tested in a parallelogram that was a mirror image of the original, the chicks originally trained to find the food in the acute corner continued to search the acute corner in the new test arena (i.e. ignoring the length of the wall), whereas those trained to find food in the obtuse corner followed the length of the wall and ended up searching around the acute corner, while when tested in a rhombus (i.e. only with angular information available) they searched correctly in the obtuse corner. These results suggest that the acute angle was a more salient geometric feature that acquired more control over the animals' behaviour than the length of the wall, whereas the obtuse angle was a less salient feature and therefore animals rather relied on the length of the wall to find the food.

In the current study, we sought to utilise the potentially differing salience of different angles in a rhombus arena to examine overshadowing of geometry learning by the presence of discrete landmarks. In Experiment 1, as a preliminary experiment, we aimed to establish that the acute and the obtuse corners in the rhombus arena in our water maze differed in their salience for rats. The results of this experiment suggested that the two corners with different angles did indeed differ in their stimulus salience. Therefore, in the subsequent two experiments we tested overshadowing of learning about these corners by the presence of discrete landmarks. We predicted that there should be more chance of observing overshadowing of the geometry by the presence of the landmark when the target geometry was the obtuse angle than when it was the acute angle, as the latter was found to be more salient than the former. In addition, in Experiment 2 we manipulated the relative validity of the target geometric cue in comparison to the landmark, in order to maximise the chance of observing overshadowing. Thus, the geometric cue was a less valid signal for the platform relative to the landmark in the experimental group but a more valid cue than the landmark in the control group, whereas the absolute predictive value of the geometry was matched between groups. Experiment 3 examined the same question in a condition where the geometric cue and the landmark signalled the presence of the platform equally well in the experimental group.

Experiment 1

An associative learning rule such as that described by Rescorla and Wagner (1972) predicts that the rate of learning about a stimulus is proportional to the salience of that stimulus, if other things are equal. Accordingly, if we are to assess the salience of two different stimuli, the simplest way is to look at the difference in the rate of learning about the two stimuli. This seemingly simple principle, however, is not always easy to test in practice when it is applied to spatial learning within a shaped environment. The major problem is that it is difficult to ensure that the animals are exposed to the different stimuli to the exact same degree as an experimenter intended, as a spatial learning task is normally an instrumental task in which the amount of exposure to different stimuli is determined by the animals' own instrumental choice rather than by a schedule arranged by the experimenter. One way to circumvent this problem is to set up a situation where animals learn about different stimuli (corners) only incidentally while they learn to follow a discrete landmark which happens to be in the two corners of interest for an equal number of occasions, thereby ensuring that animals have equal experience of these target corners. Thus, being trained to find a platform under a landmark (X) which is located either at an acute corner (A) or an obtuse corner (B), animals are exposed to a contingency that can be described as AX+ / BX+. As the development of associative strength to A and B should be proportional to the relative salience of A and B, when animals are later given a choice between A an B, the preference should be proportional to their associative strengths, hence their salience. Based on these arguments, we predicted that rats should develop a preference for the acute corner over the obtuse corner along the course of training, if the former is more salient than the latter. In order to control for any non-associative process which could be responsible for a potential preference for the acute corner, we included a control group, in which rats were trained similarly to follow the landmark but in a square arena. Both groups of animals were finally tested in the rhombus arena in the absence of the landmark or the platform.

Method

***Subjects*.** Subjects were 16, experimentally naïve, male Hooded Lister rats (*Rattus norvegicus*) obtained from Harlan, UK. They were approximately 3 months old at the start of the experiment, and were housed in pairs in a temperature-controlled room (20 °C) under 12:12 h light-dark cycle (light on at 0700) throughout the experimental period. All testing took place during the period when the lights were on in the room.

***Apparatus*.** The experiment was conducted in a white circular pool that was 2 m in diameter and 60 cm deep. The pool was filled to a depth of 30 cm with a mixture of water and white opacifier (500 ml, OP303B, supplied by Rohm and Haas, UK). This opaque mixture was maintained at a temperature of 25 °C (± 2 °C) and was changed daily. A white circular ceiling with a diameter of 2 m was suspended 1 m above the top edge of the wall of the pool. Eight 45-W spotlights were recessed in the ceiling. They were each 22.5 cm in diameter and arranged symmetrically in a 1-m-diameter circle with its centre above the centre of the pool. In the centre of the circular ceiling was a 30-cm diameter hole into which a wide-angled video camera was fixed. The image from the camera was relayed to a monitor, recording equipment, and a PC. Tracking software (EthoVision, Noldus, NL) was used to record the rats' swim paths. A grey curtain that hung from a rail around the circular ceiling at a distance of 25 cm from the edge of the pool and to 25 cm below the top of the pool wall was drawn around the pool throughout the experiment.

Four white polyurethane boards were used to create the rhombus-shaped arena. They were 1.4 m in length, 58 cm high, and 0.5 cm thick. The long (top) side of each board was attached to an aluminium bar which extended beyond the end of the board and sat on the edge of the pool, so that the entire arena could be suspended within the pool. The four boards were arranged to form a rhombus with acute and obtuse corners of 60° and 120° respectively. For a control group, a square arena (1.14 m x 1.14 m) similarly made with the same material was used.

A clear Perspex platform, 10 cm in diameter and mounted on a 1.5-cm diameter column, was submerged 2 cm below the surface of the water. The surface of the platform consisted of a series of concentric ridges. The centre of the platform was located on an imaginary line that bisected a corner, 25 cm away from the point where two walls met.

The landmark was a tennis ball painted black, 7cm in diameter, which was attached to a horizontal clear Perspex rod with a diameter of 6 mm. One end of the rod was attached through a hole drilled in an aluminium bar supporting the wall. The centre of the ball was positioned directly above the centre of the platform. The lowest vertical point of the ball was 27 cm above the surface of the water.

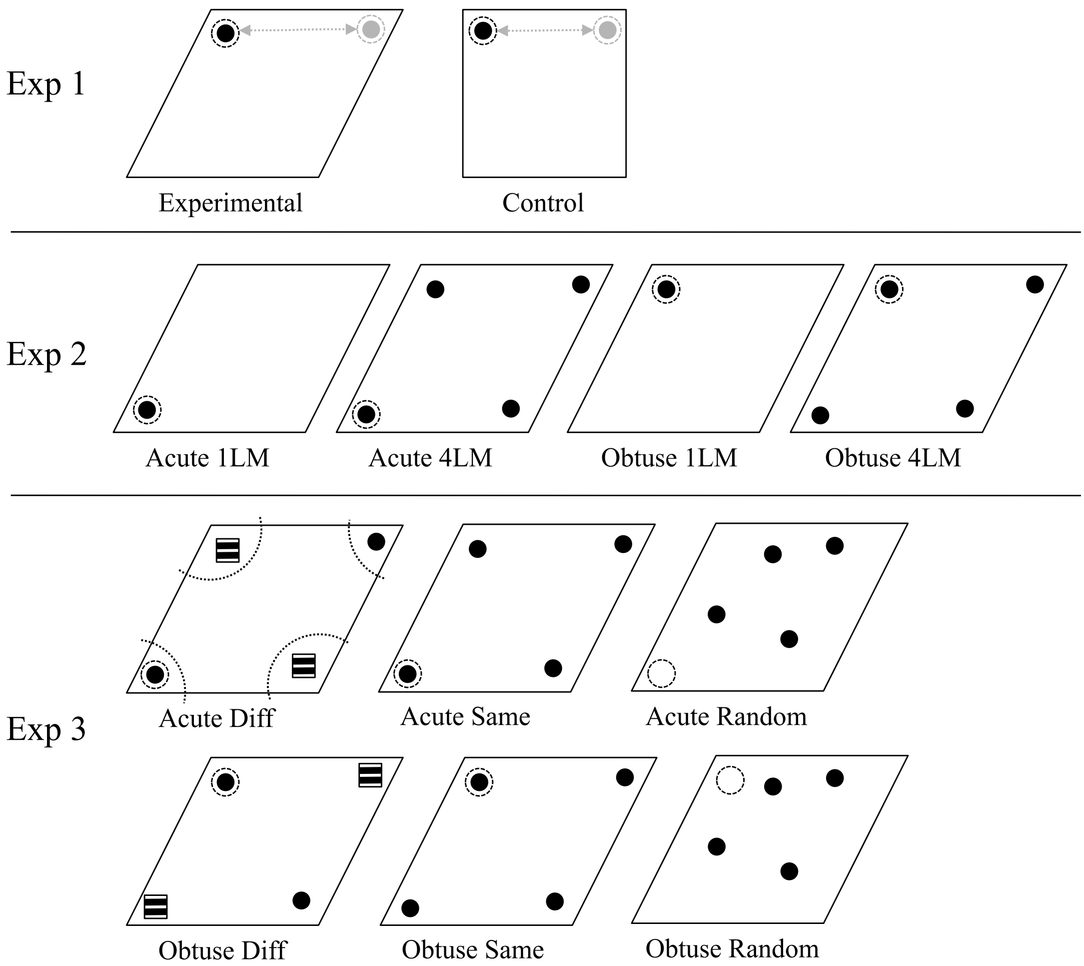

Figure 1. Schematic representation of apparatus settings for the three experiments. Circles filled in black represent spherical landmarks, whereas a circle with a dashed line represents a submerged platform. Rectangles with stripes represent the striped prism landmark used in Experiment 3. The platform was placed in one of the acute or obtuse corners throughout training depending on the group. The dashed arc at each corner of the rhombus in Experiment 3 represents a notional zone used for the analysis of initial choice during acquisition

Procedure. The rats were randomly and equally assigned to two groups at the start of the experiment (N=8). Animals in both the experimental and the control groups were trained to find a hidden platform in one corner that was always signalled by the presence of a landmark directly above the platform. The experimental group was trained in a rhombus arena, and the position of the platform and the landmark moved together from trial to trial, so that on half of the trials they were positioned in one of the acute corners while on the other half of the trials they were found in one of the obtuse corners. Shifts of the platform and landmark position across trials were made random with a restriction that the platform should not be found in the same corner on more than three consecutive trials. The control group was trained in an identical way except that the training took place in a square arena. The shift of platform and landmark position was yoked to that in the experimental group, by making each corner in the square arena correspond to a corner in the rhombus arena.

Each of the 16 sessions of training consisted of four training trials, with the exception of Sessions 8 and 16, in which there were three training trials followed by a 60-s test trial. Each training trial started with the rat being placed gently into the pool from the midpoint of one of the four walls with its head facing the wall, and ended when the rat found the submerged platform and rested there for 20 seconds. If the rat did not locate the platform within 60 s the experimenter guided the rat to it by placing a thumb in front of the rat's snout. No training was required for this treatment to be effective, and was required on a minimal number of trials at the beginning of training. Both the rhombus and the square arenas were rotated before each trial by 90, 180, or 270 degrees. The rotation was made at random with a constraint that all four orientations were used within a session, with the result that the platform moved across four different positions in the pool. In addition, the rats were released from a different wall on each trial, with the order of release walls being randomized, with the constraint that rats were released once from each wall within a session. These manipulations were undertaken to exclude the possibility that animals could use the absolute position of the platform in the pool or the vector from the release point as cues to find the platform.

The fourth trial of the 8th and 16th sessions was a probe test trial, in which animals in both groups were tested in the rhombus arena. During the probe test, the platform and the landmark were removed from the pool. Animals were released from the centre of the rhombus arena and allowed to swim for 60 seconds.

Data analysis. For measures of acquisition during training sessions, latency to find the platform was recorded. During the probe test trials, the animal's position in the pool was continuously tracked with EthoVision (version 3.1). In the subsequent off-line analyses, four zones of equal size were set at the four corners, and the time spent by animals in each zone was calculated. Each zone consisted of a circle (30 cm in diameter), the centre of which coincided with the centre of the potential position of platform during training, combined with an area closed by two tangents drawn towards the corner. This zone arrangement was used for all three experiments, unless otherwise mentioned. For statistical analyses, reliability of the effects was assessed against a Type I error rate of .05 throughout the present report.

Results and discussion

One subject from the experimental group developed a neck injury after completion of Session 11 and had to be dropped from the experiment. Therefore, from Session 12 onwards, the results presented here include data from the remaining seven rats in the experimental group.

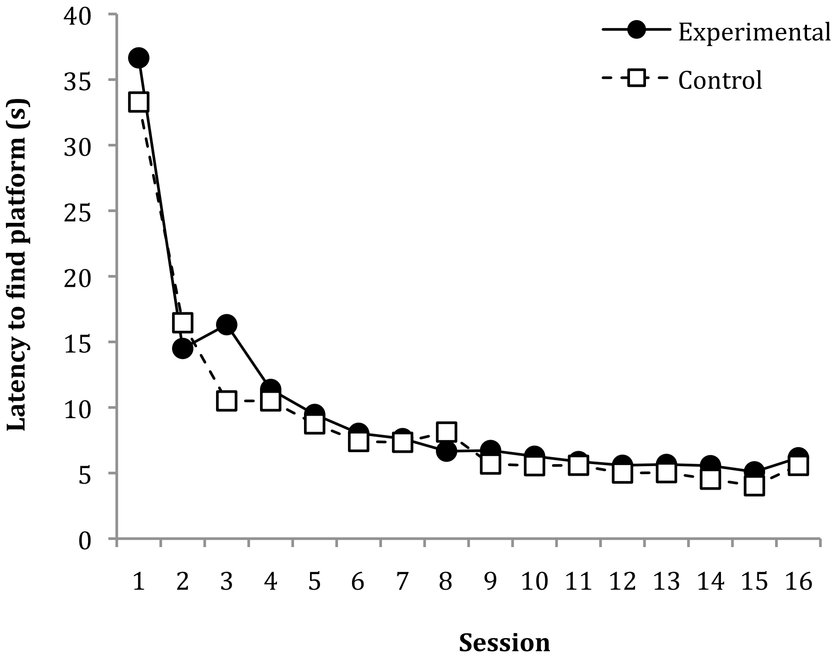

Figure 2. The mean escape latencies across 16 sessions of training in the experimental group and the control group in Experiment 1.

Figure 2 shows the mean latency to find the platform for each group across 16 sessions of training. Both groups quickly learned to find the platform under the landmark, with no difference between groups. A group x session ANOVA, with one subject with missing values being omitted, showed only a significant effect of session, $F(15,195) = 67.10$. There was no effect of group and no group x session interaction, $Fs < 1$.

Figure 3A shows the result from the first probe test conducted on the fourth trial of the eighth session. During the test trial, both groups spent more time in the acute corner than in the obtuse corner, but the preference was more prominent in the experimental group. A group x corner ANOVA revealed a significant main effect of corner, $F(1,14) = 9.14$, but the interaction was not significant, $F < 1$. However, separate comparisons between times spent in the two corners within each group revealed that the experimental group spent significantly more time in the acute corner than the obtuse corner, $F(1,14) = 7.28$, but the preference of the acute corner in the control group was not significant, $F(1,14) = 2.49$, $p > 0.1$.

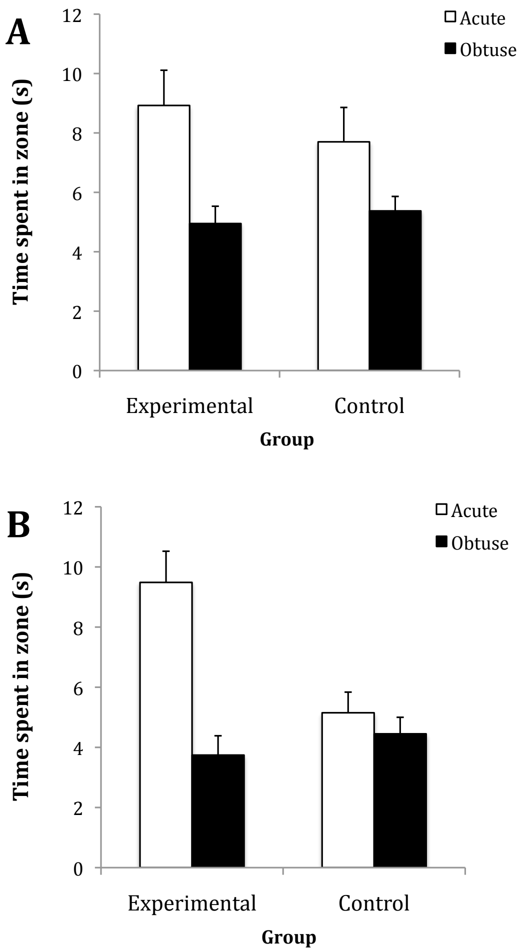

Figure 3. The mean time spent in the acute (white bars) and the obtuse (black bars) zones by the two groups in the first extinction test after 8 sessions of training (A) and in the second extinction test after 16 sessions of training (B) in Experiment 1

In order to test whether the mild preference for the acute corner shown by the control group, although statistically nonsignificant, persisted with further training, we trained the rats for further eight sessions and conducted the second test.

Figure 3B shows the results from the second probe test conducted on the fourth trial of the 16th session. The experimental group again showed a clear preference for the acute corner, whereas the control group spent roughly equal amounts of time in the acute and obtuse corners. The above description was supported by a group x corner ANOVA, which revealed a significant main effect of corner, $F(1,13) = 18.49$, group, $F(1,13) = 6.21$, and a group x corner interaction, $F(1,13) = 11.33$. Subsequent analyses of the simple main effects showed that the experimental group spent significantly more time in the acute corner, $F(1,13) = 27.55$, but the control group did not, $F < 1$. In addition, the experimental group spent more time in the acute corner than did the control group, $F(1,13) = 12.73$. To summarise, in both tests only the experimental group showed a significant preference for the acute corner, and the difference between groups was clearer in the second test.

In the current experiment, the rats were trained to find the platform under the spherical landmark suspended above the platform, which on half of the trials was located in the acute corner and on the other half of the trials in the obtuse corner. Therefore, no explicit learning was required with regard to the value of these two corners. Nevertheless, when subsequently tested in the absence of the landmark, the rats in the experimental group showed a preference for the acute corner. Crucially, such a preference was not found in the control group of which animals were trained similarly to follow the landmark but in the square arena, ensuring that the preference for the acute corner in the experimental group was a result of learning that took place incidentally in the rhombus arena. The preference for the acute corner in the experimental group, then, can be best explained if we assume that some residual associative strengths were acquired by the acute and the obtuse corners when they were paired with the platform in conjunction with the landmark, but critically at different rates; the acute corner acquired higher associative strength than the obtuse corner, which indicates that the former was more salient than the latter according to standard learning rules (e.g. Rescorla & Wagner, 1972; Miller & Shettleworth, 2007). Overall, the result is consistent with the previous report in chicks showing that the acute corner was more salient than the obtuse corner. (Tommasi & Polli, 2004). In summary, Experiment 1 confirmed the prediction that the salience of the acute corner is higher than that of the obtuse corner, and thereby warrants the question as to the possibility of differential overshadowing of geometry by discrete landmarks depending on the salience of the target geometric cue, which was examined in the following two experiments.

Experiment 2

In Experiment 2, the ability of a spherical landmark to overshadow learning based on the geometry of an enclosed arena was tested in two angular conditions; different groups of rats were trained in a rhombus arena to find a hidden platform either in an acute corner or in an obtuse corner, based on the finding that the acute corner is more salient than the obtuse corner in our rhombus arena (Experiment 1). If the relative salience of stimuli in a compound determines the degree of overshadowing (Mackintosh, 1976), then it is expected that the association between the obtuse corner and the platform would suffer from overshadowing by the presence of the landmark to a greater extent than does the association between the acute corner and the platform.

In addition, a manipulation was made to make the relative validity of the geometric cues different between the experimental and control groups. Thus, for experimental groups (Acute 1LM and Obtuse 1LM; see Figure 1), there were two identical correct corners and the platform was always located in a corner that contained the landmark, with the effect that the landmark was better correlated with the presence of the platform (100%) than were the correct geometric cues (i.e. correct corner; 50%). The two control groups (Acute 4LM and Obtuse 4LM) were trained in the same way except that identical landmarks were placed in all four corners, so that the landmark was more weakly correlated with the platform (25%) than were the correct geometric cues (50%). It should be noted that if animals learned about the geometry independently of additional information provided by the landmarks, the experimental and control groups should reveal equal learning based on the geometry, as the absolute predictive validity of geometric cues was matched in the two groups; only the presence of the landmark in different corners in the experimental and control groups made the relative validity of the geometric cues different in the two groups. In addition to the 4LM groups providing a control condition that enabled us to manipulate the relative validity of landmarks and geometry between experimental and control groups, they also provided an important control against generalisation decrement. If a no-LM control group was employed instead of the 4LM group then any overshadowing effect observed could be explained by the fact that the difference between the training and the test contexts was larger for the experimental group than for the control group, with the latter group experiencing virtually no change.

With the design as described above, two predictions were made; firstly, learning about geometry should be overshadowed by the presence of a landmark that is a better predictor of the platform’s location, and secondly, such an overshadowing effect should be stronger in the groups for whom the platform is placed in an obtuse corner which was found to be less salient in Experiment 1. On the other hand, if there was no overshadowing even under such conditions, it would provide particularly strong evidence for the claim that learning about geometry is indeed impervious to information derived from additional cues that are unequivocally non-geometric.

Method

***Subjects*.** The experiment was conducted in two replications, with 40 animals in the first and 24 animals in the second replication. As there was no effect of replication in any measures throughout the experiment, the data from the two replications were pooled for the statistical analysis and presentation. Thus, subjects were 64, experimentally naïve, male Hooded Lister rats (*Rattus norvegicus*) obtained from Harlan, UK. They were approximately 3 months old at the start of the experiment, and were housed in the same condition as in Experiment 1.

***Apparatus*.** The apparatus was identical to those used in Experiment 1, except that training and testing were conducted only in the rhombus arena.

***Procedure*.** The rats were randomly and equally assigned to four groups at the start of the experiment (N=16). Animals in two experimental groups were trained to find a hidden platform in one corner of the arena with a single landmark suspended directly above the platform (1LM). Animals in two control groups were equally trained except that four identical landmarks were suspended in four corners (4LM). Half of the animals in each of the experimental and control groups were trained with the platform placed in one of the acute corners (Acute), whereas the other half was trained with the platform in one of the obtuse corner (Obtuse). Thus, four groups were referred to as Acute 1LM, Acute 4LM, Obtuse 1LM, and Obtuse 4LM.

Each of the 16 sessions of training consisted of four training trials, with the exception of sessions 14 and 16, in which there were three training trials followed by a 60-s test trial. General training procedures, such as rotation of the arena and release point, were identical to those in Experiment 1.

On the fourth trial of the 14th session a test trial was conducted with the platform removed from the pool, but with the landmarks and walls creating the rhombus shape remaining as during the training. This test sought to ensure that 4LM control groups had learned the discrimination of the correct versus incorrect corners, because it was not evident from observing these animals during training that they were swimming directly to the corners containing the platform. Following the test trial and two sessions of retraining, finally a geometry test was conducted on the fourth trial of the 16th session, with the platform and all the landmarks removed from the pool, but with the rhombus shape remaining. In both the first and the second test trials, rats were released from the centre of the arena and allowed to swim for 60 seconds, after which they were removed from the pool by the experimenter.

Results and discussion

Figure 4 shows the mean latency to find the platform for each group across 16 sessions of training. It is important to note that direct comparisons between acute and obtuse conditions should be made with some caution because of the presence of a potentially confounding factor pertinent to the rhombus arena: the distance between the two geometrically correct corners was greater for the acute groups than for the obtuse groups, which could have resulted in longer latencies for the acute groups. Accordingly, we limited any post-hoc analyses when required to the comparisons between landmark conditions within each angle condition.

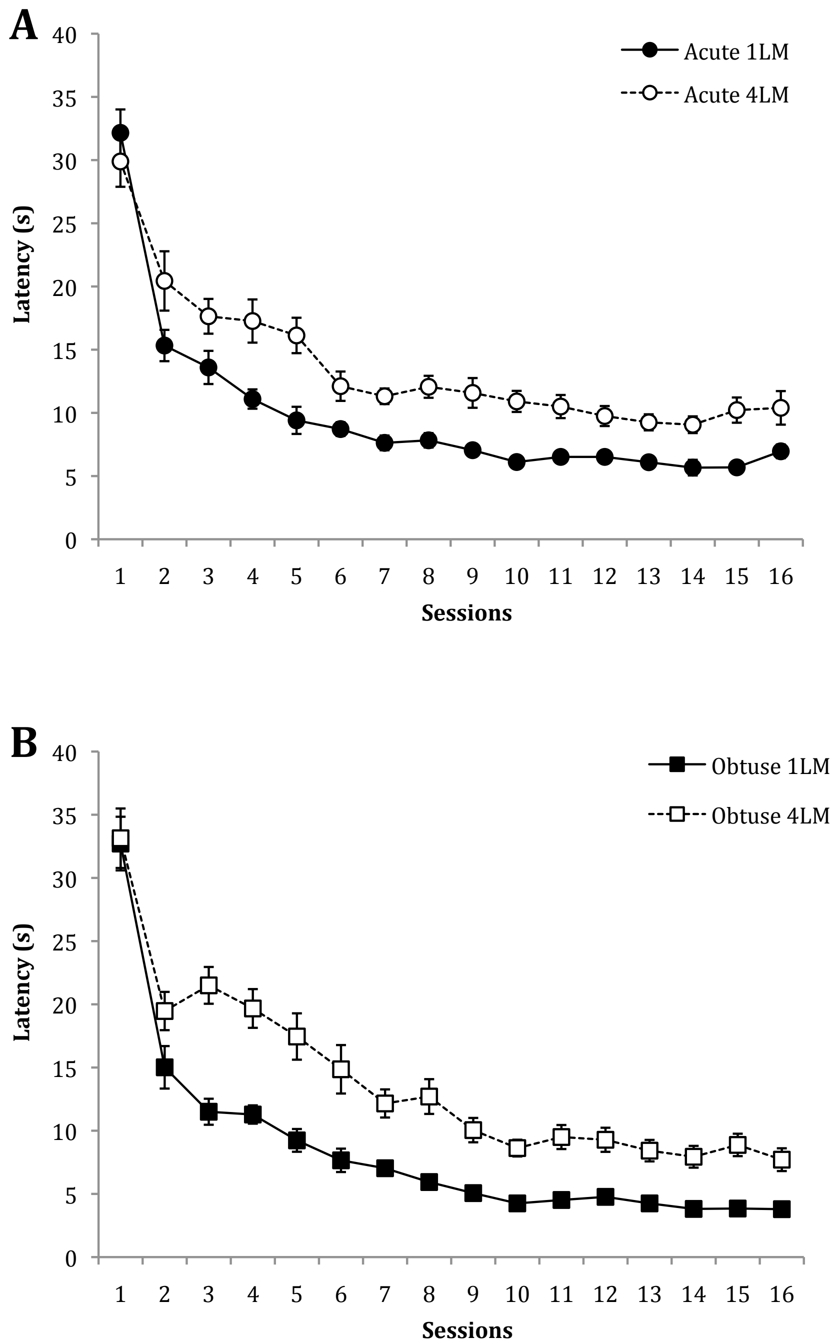

Figure 4. The mean escape latencies across 16 sessions of training in the Acute groups (A) and the Obtuse groups (B) in Experiment 2

Figure 4 shows that in both acute and obtuse conditions the presence of a single landmark above the platform facilitated acquisition of the task. A three-way ANOVA with angle and landmark as between-subjects variables and session as a repeated measure revealed a significant main effect of landmark, $F(1,60) = 123.19$ and session, $F(15,900) = 154.33$. There was also a marginally significant angle x landmark interaction, $F(1,60) = 3.34$, $p = .073$, but the simple main effect of landmark was found to be significant in both acute, $F(1,60) = 42.98$, and obtuse,

$F(1,60) = 83.55$, groups, confirming that the single landmark facilitated learning in both angle conditions.

The control over behaviour by the landmark was also evident in the first test trial, during which animals swam for 60 seconds in the presence of both landmarks and geometry, but in the absence of the platform. Unfortunately, the data from this test trial for the second replication with 24 animals were lost due to a hard disk recorder crash following the test, and therefore we present only the result based on the 40 animals run in the first replication in Table 1.

Table 1. Mean time in seconds (SEM) spent in each corner during the first probe test in Experiment 2.

	Landmark Correct	Rotational Correct	Total Correct	Total Incorrect
Acute 1LM	19.5 (1.03)	7.4 (0.53)	26.9 (0.83)	5.2 (0.43)
Acute 4LM	-	-	24.0 (0.53)	6.9 (0.51)
Obtuse 1LM	25.0 (1.17)	2.6 (0.41)	27.6 (1.04)	1.7 (0.51)
Obtuse 4LM	-	-	21.1 (1.41)	2.9 (0.61)

Note: For groups Acute 1LM and Obtuse 1LM, times spent in the landmark correct corner and the rotational correct corner are presented separately from the total time spent in the correct corners.

The animals in the 1LM groups preferentially explored the corner with a landmark. In addition, the behavioural control exerted by the landmark was more marked in Obtuse 1LM than in Acute 1LM. Time spent in each corner was compared between Acute 1LM and Obtuse 1LM with an angle x corner ANOVA, contrasting the geometrically correct corner with a landmark, the geometrically correct corner without a landmark (the rotational correct corner), and the mean of the two geometrically incorrect corners. This revealed a significant effect of corner, $F(2,36) = 250.30$, and an angle x corner interaction, $F(2,36) = 14.71$. Subsequent analyses showed that Acute 1LM spent less time in the landmark correct corner than did Obtuse 1LM ($p < 0.05$), but they spent more time in the rotational correct corner and also in the incorrect corner than did Obtuse 1LM ($ps < 0.01$). Both groups, in turn, spent more time in the landmark correct corner than in the rotational correct corner ($ps < 0.001$). An overall analysis including 4LM control groups with angle x landmark x zone (geometrically correct vs geometrically incorrect) ANOVA revealed a significant landmark x zone interaction, $F(1,36) = 13.63$, with 1LM groups spending more time in the geometrically correct corners overall than did 4LM groups, $F(1,36) = 13.67$, and less time in the incorrect corners, $F(1,36) = 4.62$. More important for the purpose of this probe test was that 4LM control groups spent more time in the correct than the incorrect corners, $F(1,36) = 226.73$, thereby demonstrating a good discrimination of different angles.

Taken together, these findings from the training stage suggest that the single landmark above the platform did acquire a good control over animals' behaviour, in addition to the control exerted by the geometry of the arena.

Geometry Test

The question of primary interest was whether learning based solely on the geometry of the arena was restricted by the presence of a landmark during training. The result from the geometry-only test, which is the critical test to the question just mentioned, is presented in Figure 5. The figure shows that all groups of animals discriminated the correct from incorrect corners, and more importantly, that such discrimination was less marked in animals in 1LM experimental groups than in animals in 4LM control groups. This observation was supported by an angle x landmark x zone ANOVA, which showed a significant main effect of angle, $F(1,60) = 114.07$, landmark, $F(1,60) = 4.66$, zone, $F(1,60) = 329.64$, and more importantly a landmark x zone interaction, $F(1,60) = 15.67$. Subsequent analyses of simple main effects on this interaction revealed that 1LM groups overall spent significantly less time in the correct zones than did 4LM groups, $F(1,60)=15.14$, and spent more time in the incorrect zones than did 4LM groups, $F(1,60)=6.85$. The result indicates that overall, the presence of the single landmark overshadowed learning about geometry.

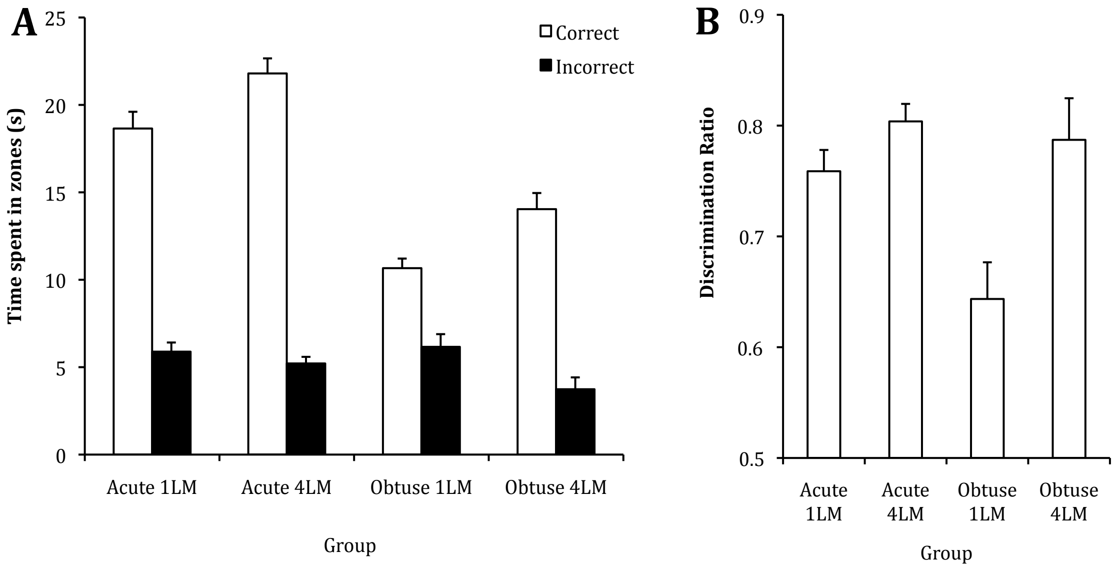

Figure 5. A: The mean time spent in the correct (white bars) and the incorrect (black bars) zones by the four groups during the geometry test in Experiment 2. B: The mean discrimination ratio for the four groups during the geometry test in Experiment 2

Although the difference between 1LM and 4LM appeared to be greater in the obtuse condition than in the acute condition, an angle x landmark x zone three-way interaction was not significant, $F<1$. In order to examine more directly the potential difference in the size of the overshadowing effect between the two angular conditions, we calculated a discrimination ratio for each animal by dividing the time spent in the correct corner by time spent in both the correct and the incorrect corners. Figure 5B suggests that the difference between 1LM and 4LM was larger in the obtuse groups than in the acute groups. An angle x landmark ANOVA revealed a marginally significant interaction, $F(1,60) = 3.11$, $p = 0.08$. Subsequent comparisons within each angular condition revealed that the difference between 1LM and 4LM groups was significant in the obtuse groups, $F = 13.20$, but not in the acute groups, F

= 1.29, $p > 0.1$. Thus, the results lend some support to our second prediction that the overshadowing of geometry should be a function of the salience of the target geometry.

It should be noted that there is one potential factor that might explain why the difference in the size of overshadowing effect between angular conditions failed to reach statistical significance. It might be the case that the presence of the landmark not only restricted learning about geometry in the 1LM experimental groups but also learning in the 4LM control groups to some extent, with the size of such a restriction being larger in the Obtuse 4LM than in the Acute 4LM group. In other words, learning about geometry was already overshadowed in the Obtuse 4LM control group, thereby reducing the size of the difference between Obtuse 1LM and Obtuse 4LM. An inspection of the data from the first and the second probe tests (Table 1 and Figure 5) supports such a claim. The first test was conducted with both geometry and landmarks present, whereas the second test was with geometry only. The rats in Acute 4LM were not affected much by the omission of the landmarks in the second test, whereas rats in Obtuse 4LM performed in the second test considerably worse than in the first test. Time spent in the correct corners during the second test, expressed as a percentage of that in the first test, was 91.0 % for Acute 4LM and 71.4 % for Obtuse 4LM. The difference was statistically significant (two-tailed independent t-test, $df = 18$, $t = 2.78$, $p < 0.05$). Thus, the presence of landmarks, albeit being less informative than the different angles, still affected learning about geometry in Obtuse 4LM, which can account for the lack of a significant difference in the size of overshadowing effect between acute and obtuse conditions. There are several possible reasons why the presence of identical landmarks at four corners can overshadow learning about obtuse corner, but one can point out that the presence of the landmark was still to some extent correlated with the presence of the platform, albeit less so than in the experimental group. Moreover, such a correlation could actually have been higher than the nominal value of 25 % depending on the actual stimulus contingency animals experienced. This potential problem of practical contingency and overshadowing in the control group was explicitly taken into account in the final experiment.

Whatever the merit of these analyses, to summarise we demonstrated overshadowing of learning about the geometry by the presence of a single landmark above a platform in Experiment 2. To our knowledge this is the first demonstration of overshadowing of geometry learning by discrete landmarks in male rats. Moreover, the overshadowing effect tended to be larger in the obtuse condition than in the acute condition. It is unlikely that overshadowing was a result of a difference in performance level during training, as throughout training the 1LM groups showed better overall performance than 4LM groups. It is also unlikely that the overshadowing was produced by different levels of generalisation decrement resulting from physical changes of contexts from training to the test, as it was 4LM control groups that experienced the greater change, with the removal of four landmarks, than did 1LM groups. Overall, in the current experiment we found that a discrete landmark is capable of overshadowing learning based on the geometry of the arena when it is more valid a cue for the goal than the geometry. Before going into further discussion on the implication of the results, we report the final experiment that examined the same question of overshadowing of geometry learning in conditions where predictive validities of the geometric cues and landmarks were matched in the experimental groups.

Experiment 3

In Experiment 3, we tested whether discrete landmarks are capable of overshadowing learning based on geometry when the landmarks and the geometric features of the arena predicted the presence of the platform equally well in the experimental groups. The question is important as many previous studies employed just such a condition in which the predictive validity of the landmarks and geometric features were matched, and they failed to demonstrate overshadowing (e.g., Hayward et al., 2003; McGregor et al., 2009).

For the two experimental groups (Acute Diff and Obtuse Diff), two different pairs of identical landmarks were used, whereby each pair of landmarks was associated with either the acute or the obtuse corners (see Figure 1). For the two control groups (Acute Same and Obtuse Same), all four landmarks were identical, a condition identical to the control groups in Experiment 2. These arrangements ensured that the geometry was the more reliable predictor of the platform than the landmark in the control groups whereas the identities of the landmarks and the geometry were equally valid predictors of the platform in the experimental groups.

In addition, based on the suggestion made in the last experiment that the obtuse control group might also have suffered from overshadowing, we included two further control groups, Acute Random and Obtuse Random. These random control groups were trained in the same way as the former two control groups, except with the use of four identical landmarks suspended from the ceiling at random positions within the rhombus arena, which were moved from trial to trial so that these landmarks had no bearing either to the position of the platform or to the four corners of the rhombus. Thus, if, for whatever reason, the presence of the four identical landmarks at the four corners overshadowed learning about geometry and thereby masked the difference in geometry learning between the experimental and control groups in the last experiment, the random control groups should be free from such an effect. Therefore a greater difference between experimental groups and the random control groups was expected when rats were tested in the presence of only the geometric cues in Experiment 3. Because the results of this test indicated such a result, a further test was conducted at the end of the experiment in a square arena with the landmarks from training present in two adjacent corners. This test enabled us to assess the extent to which experimental and control animals learned about landmarks, which in turn would provide information as to the relationship between learning about landmarks and learning about geometry.

Method

***Subjects*.** Subjects were 72, experimentally naïve, male Hooded Lister rats of approximately 3 months at the start of the experiment. They were housed in identical conditions to those in the previous experiments.

***Apparatus*.** The apparatus was identical to those used in Experiments 1 and 2, except that two different sets of landmarks were used. A foam ball painted in black (10 cm diameter) served as one type of landmark. The other landmark was an octagonal prism, with each of the eight rectangular panels measuring 4 cm wide x 10 cm high x 1 cm thick, that was made of polystyrene and was hollow inside. The outer surface of the eight sides of the prism was continuously painted with horizontal stripes of black and white (2-cm wide each stripe). An opaque plastic plate covered the top of the prism whereas the bottom was open so that the inside, which was entirely white, was visible from underneath. For groups Diff and Same, the landmarks were attached to the top end of the walls of the rhombus arena with a transparent plastic rod so that the bottom edge of the two landmarks was at the same height (26 cm above the water). For the Random groups the same landmarks as those used for groups Same were suspended from the ceiling of the pool by thin metal wires that were painted white. The landmarks were set at the same height as those in the other four groups. During the landmark test conducted at the end of the experiment, a square arena identical to that used in Experiment 1 was used. Two different landmarks were suspended at two adjacent corners of the square, with the positions of the two landmarks counterbalanced within each group.

***Procedure*.** At the start of the experiment rats were randomly assigned to one of six groups (N=12 each). The general training and test procedures were identical to Experiment 2. Half of the rats were trained with the platform in one of the acute corners (groups Acute) and the other half with the platform in one of the obtuse corners (groups Obtuse). The experimental groups (Acute Diff and Obtuse Diff) had two identical landmarks in the geometrically correct corners and two identical landmarks of the different variety in the incorrect corners, whereas Same control groups (Acute Same and Obtuse Same) had identical landmarks in each of the four corners. The random control groups (Acute Random and Obtuse Random) had four identical landmarks suspended from the ceiling at positions picked randomly from 40 potential positions, and the positions of the four landmarks were different in every trial. The landmark was never positioned directly above the platform for these random groups, and the average distance between the platform and the nearest landmark was 39 cm for Acute Random and 26 cm for Obtuse Random. The use of the black ball and the striped prism as the four landmarks was counterbalanced within each control group. Also, the use of the black ball and the striped prism as the landmark above the platform was counterbalanced within each experimental group. In addition to the latency score, a record was taken on each trial of the corner of the pool the rat entered first after release, in order to assess more accurately the contingencies experienced by rats in different conditions. An entry (henceforth referred to as a choice) was recorded if the rat's snout entered a notional arc with a radius of 40 cm and its centre at the point where the walls creating the corner met.

Following 16 sessions of training, all groups of rats received a single 60-s geometry test in the absence of the platform and the landmarks, in the same manner as in Experiments 1 and 2. In the session following the geometry test, rats in groups Same and Diff were given a single 60-s landmark test. The landmark test was conducted in a square arena with two different landmarks suspended at two adjacent corners. For groups Diff, the two landmarks were the correct and the incorrect landmarks, whereas for groups Same, one of these landmarks was familiar but the other was novel. With only two of the four corners containing a landmark, the test was also designed to detect the preference for landmarks in general, in addition to the preference specific to the landmark associated with the platform during training.

Results and discussion

Acquisition

Figure 6 shows the acquisition data for each group of animals across 16 sessions of training. In the acute groups, variety or spatial arrangement of landmarks did not affect the acquisition rate. By contrast, the presence of landmarks in the corners, including one directly above the platform, helped animals in Obtuse Same and Obtuse Diff to find the platform faster than animals in Obtuse Random. Also, Obtuse Diff outperformed Obtuse Same early in training. An angle x landmark x session ANOVA conducted on latencies (Figure 6 A and B) revealed a significant effect of landmark, $F(1,66) = 44.77$, as well as an angle x landmark interaction, $F(2,66) = 25.91$. A simple main effect of landmark was significant in the Obtuse groups, $F(2,66) = 69.33$, but not in the Acute groups, $F(2,66) = 1.35$, confirming the above description. Pairwise comparisons confirmed that Obtuse Random was significantly slower to find the platform than the other two groups, in which Obtuse Diff was overall faster than Obtuse Same at a marginally significant level, $p = .09$.

In addition to the escape latency, we also analysed the choice accuracy by scoring the frequency of animals' entering the correct corner first in each trial, in order to better understand the role of practical contingency as discussed in the previous experiment. The analysis of the choice measure (Figure 6 C and D) revealed a similar pattern of results to that for the latency; there was a significant effect of landmark, $F(2,66) = 6.27$, as well as a significant angle x landmark interaction, $F(2,66) = 3.23$. The main effect of landmark was only significant in the obtuse groups, $F(2,66) = 9.13$ ($F < 1$ for the acute groups). It should be noted that the overall difference between the acute and the obtuse groups could have reflected an artefact from that the animals in the acute groups tended to swim closer the wall and consequently swim through the obtuse corner to reach one of the acute corners, not necessarily searching for a platform around the obtuse corners, thereby reducing the overall choice accuracy. For this reason we refrained from a direct comparison across angular conditions, and limited post-hoc analyses only to the comparisons between landmark conditions within each angular condition. To summarise, different arrangements of the landmarks affected the performance during acquisition in the obtuse groups, but not in the acute groups. Within the obtuse groups, the overall choice accuracy for Obtuse Random was significantly lower than Obtuse Same and Obtuse Diff ($ps < .01$), whereas the difference between the latter two groups failed to reach statistical significance ($p = .13$), despite the apparent difference early in training.

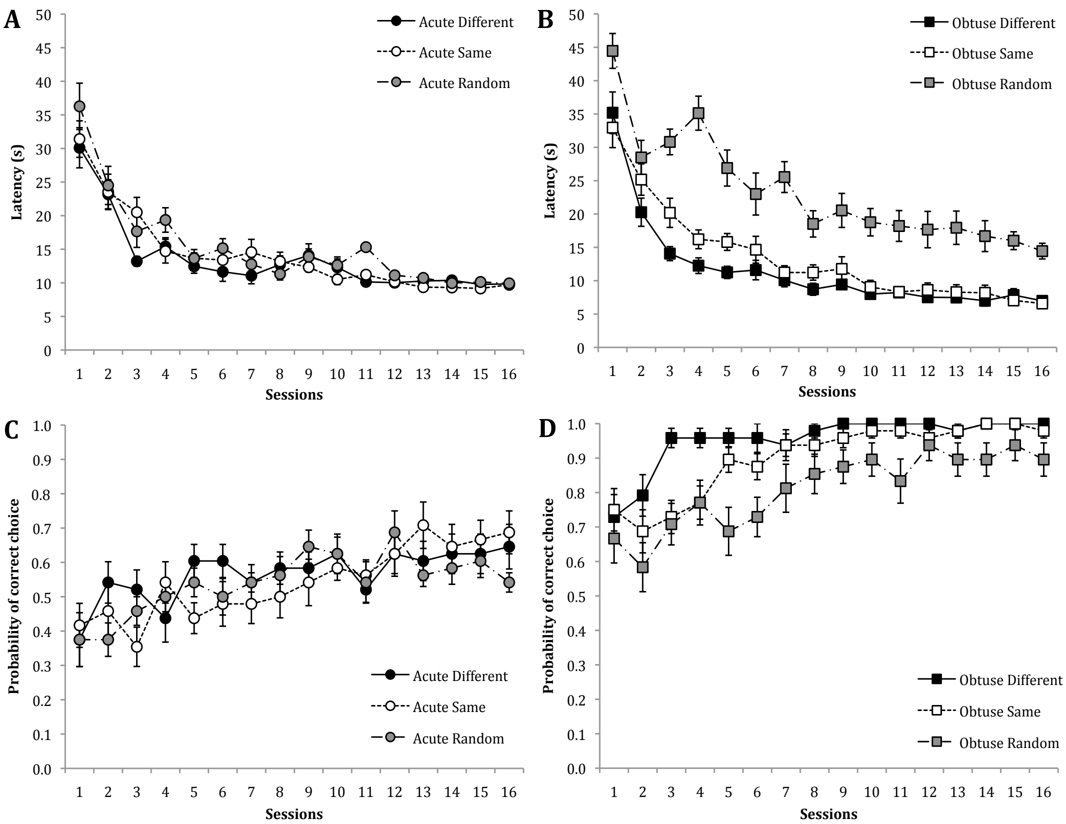

Figure 6. A and B: The mean escape latencies across 16 sessions of training in the acute groups (A) and the obtuse groups (B) in Experiment 3. C and D: The mean rates of correct first choice in the acute groups (C) and the obtuse groups (D).

Geometry Test

The results of primary interest, from the geometry test, are presented in Figure 7. The performance of the three acute groups did not differ from each other, whereas Obtuse Random spent more time in the correct zone than the other two obtuse groups. This description was supported by a three-way ANOVA, which showed an angle x landmark x zone three-way interaction, $F(2,66) = 3.33$, in addition to the main effect of zone, $F(1,66) = 551.52$, angle, $F(1,66) = 139.01$, and landmark, $F(2,66) = 6.77$. Subsequent analyses of simple main effects showed that the effect of landmark was significant only in the Obtuse groups and in the time spent in the correct zone, $F(2,66) = 9.24$, but not in the incorrect zone or in the Acute groups in either zone (Fs < 1.23). Subsequent comparisons in the Obtuse groups confirmed that Obtuse Random spent significantly more time in the correct zone than did Obtuse Same and Obtuse Diff (ps < .01), which themselves did not differ significantly (p > .1).

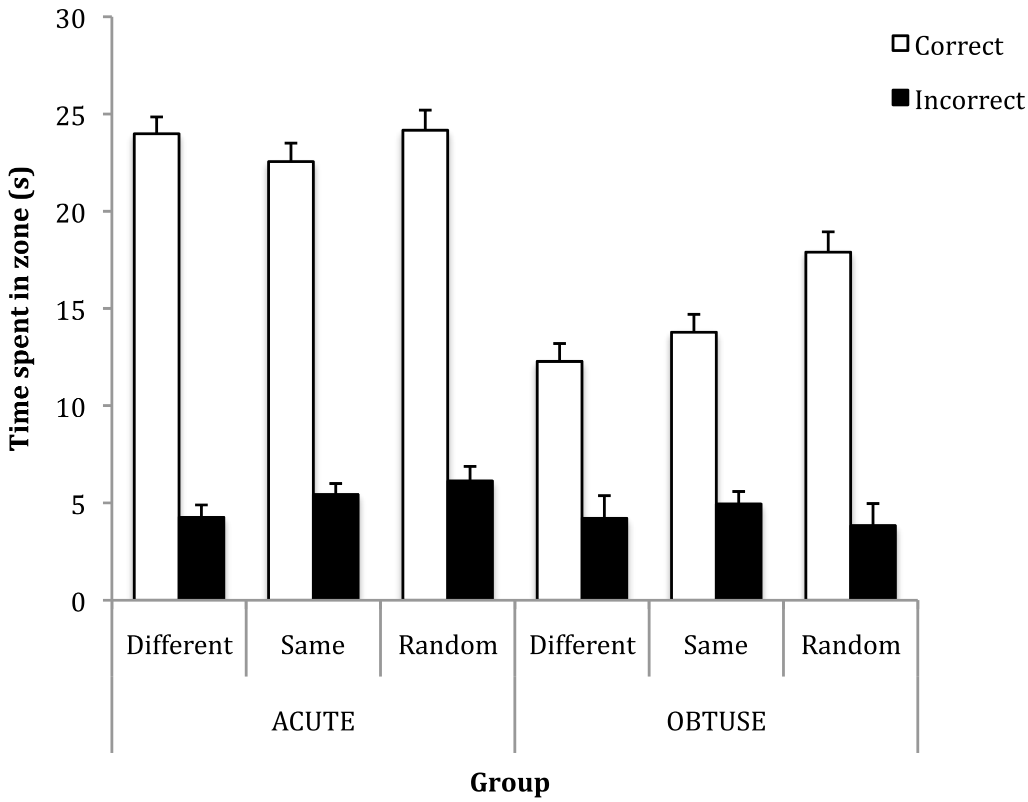

Figure 7. The mean time spent in the correct (white bars) and the incorrect (black bars) zones by the six groups during the geometry test in Experiment 3.

The primary finding in the current experiment is that during the geometry test Obtuse Random performed better than Obtuse Diff, indicating an overshadowing effect. In addition, Obtuse Random was also better than Obtuse Same, while Obtuse Same and Obtuse Diff did not differ from each other. These results suggest that the performance of rats in Obtuse Same also suffered from overshadowing by the presence of the landmark directly above the platform to the same extent as those in Obtuse Diff, thereby making it difficult to detect the overshadowing effect present in Obtuse Diff. In stark contrast to this, there was no hint of such an effect in the acute condition; the arrangement of landmarks had no effect at all on the overall acquisition rate or on the test performance. This differential overshadowing effect is indeed in support of our original prediction that the presence of landmarks should overshadow learning about the less salient obtuse corners but not the more salient acute corners.

The finding that Obtuse Different and Obtuse Same performed at a similar level during the geometry test will require some comments. As can be seen in Figure 6, after Session 6 in training these two groups showed nearly perfect choice accuracy with no difference between groups, which means that the animals in these two groups were exposed to virtually the identical practical contingency during the last 10 sessions, being almost exclusively limited to experiences in the obtuse corners. This sufficiently explains the absence of difference between these two groups at the geometry test (i.e. apparent lack of overshadowing), and also explains why these groups together performed worse than Obtuse Random: Obtuse Same and Obtuse Diff suffered from a general overshadowing effect due to the presence of a landmark above the platform. Some comment should also be made as to why Obtuse Random performed poorly during training, in terms of both latency and choice accuracy, but spent significantly more time in the correct corners than the other two groups during the test trial. Even though the landmarks did not provide information about the location of the platform in this group, these animals, typically, when they failed to find the platform in one of the corners, followed a landmark and searched around it. We observed that this unrewarded response of following the landmark persisted and thereby resulted in longer latencies in this group. In addition, we might suppose that the salience of an obtuse corner-landmark compound (for Obtuse Same and Obtuse Diff) was much higher than that of an obtuse corner alone (for Obtuse Random). If this were the case learning should take place much faster to the compound, as reflected in the actual acquisition data, but it does not necessarily mean that the obtuse corner alone in the compound-trained groups (Obtuse Same and Obtuse Diff) acquired higher associative strength than the same corner in the random group, as we found in the geometry test. Such an analysis is also consistent with the finding that there was no difference among the acute groups during training, possibly because the acute corner alone was salient enough to support maximum learning.

<u>Landmark Test</u>

Figure 8 shows the result from the landmark test. Both Acute Diff and Obtuse Diff showed a good discrimination between the correct and the incorrect landmarks, with the effect more substantial in Obtuse Diff. It can be seen that acute groups overall spent equal amounts of time in corners with and without a landmark (LM vs Rotational), whereas obtuse groups showed overall preference for the corners with a landmark. For a statistical analysis, an angle x training landmark (Same vs Diff) x landmark presence (LM vs rotational) x corner type (correct/familiar vs incorrect/novel) four-way ANOVA was conducted. The analysis revealed a significant angle x landmark presence interaction, $F(1,44) = 20.93$, where the simple main effect of landmark presence was significant in the obtuse groups, $F(1,44) = 39.90$, but not in the acute groups, $F < 1$, confirming that the animals in the obtuse, but not acute, groups showed a general preference for the corners with a landmark over the other corners without a landmark. There was also a training landmark x landmark presence x corner type interaction, $F(1,44) = 9.68$, as well as a marginally significant four-way interaction, $F(1,44) = 3.35$, $p = .07$. The analysis of the simple main effect of corner type confirmed that both Acute Diff and Obtuse Diff spent significantly more time in the correct LM corner than in the incorrect LM corner ($F(1,44) = 6.46$ for Acute Diff and $F(1,44) = 21.65$ for Obtuse Diff), thereby demonstrating discriminations between the correct and incorrect landmarks, but neither Acute Same nor Obtuse Same showed such a preference between the two landmarks, one familiar and the other novel, Fs < 1.25. More importantly for these two control groups, the preference for the landmarks in general was significant in Obtuse Same, $F(1,44)=12.34$, but not in Acute Same, $F<1$.

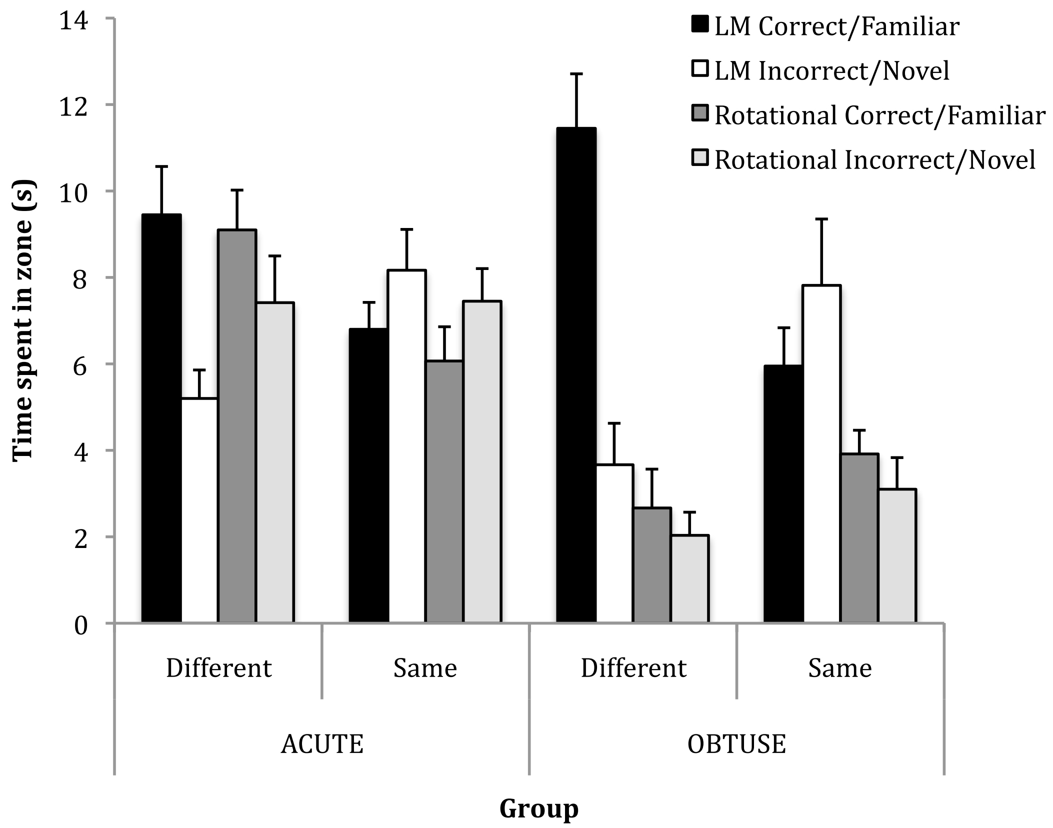

Figure 8. The mean time spent in the four corners of a square arena by each group during the landmark test in Experiment 3. *LM Correct/Familiar corner*: a corner with a landmark that was the correct landmark during training for groups Different and the landmark that accompanied the four corners during training for groups Same. *LM Incorrect/Novel corner*: a corner with a landmark that had been incorrect during training for groups Different and was a novel landmark that had never been experienced during training for groups Same. *Rotational Correct/Familiar corner*: a corner without a landmark, diagonally opposite to LM Correct/Familiar corner. *Rotational Incorrect/Novel corner*: a corner without a landmark, diagonally opposite to LM Incorrect/Novel corner

The finding that Obtuse Same, but not Acute Same, showed a general preference for landmarks is consistent with the idea that the landmarks in the four corners of the rhombus arena, albeit identical, acquired some associative strength in Obtuse Same, which was responsible for the lack of difference between Obtuse Diff and Obtuse Same in the present experiment, and also for the reduced size of overshadowing in Exp 2 as these identical landmarks overshadowed learning about obtuse corners.

General Discussion

The current set of experiments re-examined the idea proposed in the geometric module hypothesis that learning based on the geometric features of an enclosed arena is independent of learning that takes place with reference to other non-geometric features of the arena. We used discrete landmarks as non-geometric cues and differently angled corners in the rhombus arena as geometric cues. Overall, contrary to the above notion, we demonstrated that the learning based on the geometry of the arena can be overshadowed by the presence of discrete landmarks.

After establishing in Experiment 1 that the acute and the obtuse corners in our rhombus arena were indeed different in their stimulus salience, we demonstrated in Experiment 2 that a single spherical landmark suspended above a hidden platform was capable of overshadowing learning based on the geometry (angles of the corners) when predictive validities of the landmark and the geometric cues were arranged so that the landmark predicted the presence of the platform better than did the geometric feature in the experimental group, but vice versa in the control group. With respect to our second prediction that such an overshadowing effect should be more prominent when the target geometric cue was the less salient obtuse corner, we did find just such a tendency with the obtuse groups showing a greater overshadowing effect, but the effect was not statistically reliable. The final experiment, however, revealed that the relatively weak nature of the stimulus salience effect in Experiment 2 was due to an artefact produced by the fact that the learning based on the geometry in the acute and obtuse control groups were differentially affected by the presence of albeit identical landmarks at the four corners; Obtuse Same (identical to Obtuse 4LM in Experiment 2), but not Acute Same, suffered from overshadowing itself, as evidenced by the comparisons of this group's performance with the random control groups in Experiment 3. Critically, Obtuse Random, but not Acute Random, performed better than its corresponding experimental group in the geometry test, demonstrating the differential overshadowing effect depending on the relative salience of the target geometry. It is worth noting that despite the landmarks failing to overshadow learning about the acute corner in Experiment 3, there was a significant overall overshadowing effect in Experiment 2, with the size of overshadowing in the acute groups not statistically different from the overshadowing effect in obtuse groups (at least when measured with the absolute time spent in correct and incorrect zones). These findings might initially appear to be inconsistent, but they most likely reflect the difference in relative validity of competing cues between the two experiments. Thus, the current set of experiments has shown that if, and only if, the landmark was a more valid cue than the acute corner, as in Experiment 2, then the discrete landmark can overshadow learning about the acute corner, which is otherwise more difficult to overshadow due to its higher salience.

Overall, these findings support the view that learning based on the geometry of an enclosed arena follows the same principle of learning as those described in associative learning theories, in that it is sensitive to the relative validity as a predictive cue in reference to additional cues (Wagner et al., 1968), and that whether such cue competition effect occurs also depends on the relative salience of competing cues (Mackintosh, 1976). If the argument presented above is correct, it naturally leads to a question as to why previous studies failed to show overshadowing of learning based on the geometry by non-geometric cues, especially by discrete landmarks or beacons (Hayward et al., 2003; Hayward et al., 2004; McGregor et al., 2009; Pearce et al., 2001). Based on the findings from the present study, we can point out several potential variables that may account for the lack of overshadowing in the previous studies.

Firstly, it is important to acknowledge the nature of the water maze task and other free-choice navigation tasks as an instrumental conditioning task, where Pavlovian stimulus-stimulus contingencies, with which the experimenter seeks to test a cue-competition effect, is in practice determined by animals' instrumental performance. As the comparison between Obtuse Same and Obtuse Diff in Experiment 3 implied, the nature of such a task can be a problem typically when animals are trained to an asymptotic level where the instrumental choice becomes invariably accurate, thereby biasing animals' experience only to a part of the complete set of Pavlovian contingencies that the experimenter has originally arranged (see March, Chamizo, & Mackintosh, 1992 for a similar argument). It is therefore probable that, in previous studies that failed to show overshadowing, the practical contingencies that experimental and control animals experienced were similarly restricted as a result of asymptotic training with highly accurate instrumental choice performance, which might consequently have made the practical Pavlovian contingencies in the two groups very similar and therefore masked the potential overshadowing effect (e.g. McGregor et al., 2009).

Secondly, the current set of results suggests that the frequent lack of overshadowing in previous studies could have been the result of the geometric cue simply being more salient than competing non-geometric cues, especially discrete landmarks. The results from Experiment 3 lend good support to this claim. Thus, the presence of additional information provided by different types of landmarks, or indeed any landmarks suspended at corners, overshadowed learning about the obtuse corner, but failed to overshadow at all learning about the acute corner. The result is consistent with a previous report that chicks in a parallelogram arena relied more on angular information provided by corners when they were trained to find food in an acute corner, but preferred using information provided by length of the walls when they were trained to find food in an obtuse corner, indicating that the acute corner is more salient than the obtuse corner (Tommasi & Polli, 2004). In addition, Rodriguez, Chamizo, and Mackintosh (2011) recently demonstrated overshadowing and blocking of geometry by a landmark in female rats, but not in males, whereas overshadowing and blocking of a landmark by geometry was found in males, but not in females. The authors claim that these differences in cue competition effects reflect differences in the relative salience of landmarks and geometry for males and females (Rodriguez, Torres, Mackintosh, & Chamizo, 2010). Rodriguez et al. (2011) therefore propose that it is unlikely that landmarks restrict learning about geometry in male rats. Our findings, however, show that landmarks can overshadow learning about geometry in males if the salience of geometry is manipulated directly. Rodriguez et al.'s (2011) findings further suggest a possibility of reciprocal overshadowing in our studies depending on the relative salience of geometric and non-geometric cues. Although we did not have control groups against which to test the overshadowing of landmarks by the geometric cues (e.g., with geometric cues being present but irrelevant in a control group), a comparison between acute and obtuse groups during the landmark test conducted in the square arena in Experiment 3 gives us some idea about this issue. Thus, the animals in the obtuse groups overall relied on the landmarks to a greater extent than did the animals in the acute groups. In fact, the acute groups explored equally the corners with and without landmarks in the square arena. This is the reverse of the observation that learning about the acute corners was more resistant to overshadowing by the landmarks, and thus suggests the reciprocity of cue-competition between geometric and landmark cues. Taken together, these findings support the view that a potential difference between geometric and non-geometric cues can be understood by their relative salience as cues, without necessarily assuming a qualitatively different nature for the geometric cues.

Overall, the successful demonstration of overshadowing using discrete landmarks in the current study not only extends the generality of some recent studies demonstrating cue interaction between non-geometric features provided by wall colour and the geometric cues provided by their lengths (e.g., Graham et al, 2006; Pearce et al. 2006), but addresses more directly those theories, such as Wang and Spelke's (2002, 2003), that claim that discrete objects inside a bounded environment are processed in a fundamentally different and independent way to learning based on boundaries. Indeed, it may be that in those studies that utilised wall colour as the non-geometric cue the colour of walls could be processed as part of a 'modified' geometric module. As Cheng and Newcombe (2005) suggested, the representation of geometry from the shape of the environment may incorporate information provided by the non-geometric cues that create the shape. It seems plausible that this integrated representation is more readily formed when the non-geometric cues are integrated into the boundary itself, as in the case of colour cues. In contrast, the current experiments demonstrate cue competition without such a clear method of integration. Furthermore, the current study not only provides evidence for such cue competition using discrete landmarks, but also reveals the conditions under which overshadowing of geometry by landmarks is expected to be present, and where it should be absent, with the conditions proved to be in compliance with basic rules offered by associative learning theories.

In conclusion, in the present study we have demonstrated that learning based on the geometric information provided by the shape of an enclosed arena can be overshadowed by the concurrent presence of discrete landmarks. The effect was sensitive to the relative validity of geometric cues in relation to the landmarks, as well as the relative salience of those competing cues. These findings complement the recent report that a discrete landmark is able to block subsequent learning about the geometry of an arena (Horne & Pearce, 2009). Together with other recent findings on cue-interactions in a geometric learning paradigm (Graham et al., 2006; Gray, Blomfield, Ferrey, Spetch, & Sturdy, 2005; Horne & Pearce, 2011; Pearce et al., 2006; Rodriguez et al., 2011) our findings corroborate the view that spatial learning based on the geometry of an environment is controlled by the same general principles of learning that apply to other learning paradigms, and more importantly provide some resolution to inconsistencies reported from studies of cue competition in geometry learning.

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